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Feedlot performance, feed efficiency reranking, carcass traits, body composition, energy requirements, meat quality and calpain system activity in Nellore steers with low and high residual feed intake ☆

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ABSTRACT

The aim was to evaluate growth, carcass traits, feed efficiency reranking, body composition, calpain system activity and meat quality in Nellore steers that were phenotypically ranked for high and low residual feed intake (RFI). Seventy-two Nellore steers (16–21 month-old, 334 ± 19 kg BW) had free access to a feedlot diet for 70 d (feeding period 1, P1). Daily dry matter intake (DMI), body weight gain (ADG) and ultrasound carcass traits were measured individually. The 12 lowest and the 12 highest RFI steers were classed as low- and high-RFI groups and were fed for a second feeding period (feeding period 2, P2). Spearman's rank correlation was performed for RFI and gain-to-feed ratio (G:F) measured over P1 and P2. The carcass traits, meat quality and calpain system activity were evaluated at slaughter, and body composition was determined. In P1, low-RFI steers had greater G:F (0.159 vs. 0.134; $P<0.001$), lower DMI (9.30 vs. 11.1 kg/d; $P<0.0001$), lower RFI (-0.80 vs. 0.85 kg/d; $P<0.0001$), and tended to have lower rates of rump fat gain (4.48 vs. 6.05 mm; $P=0.06$), but no differences were observed for ADG, BW, and other traits measured by ultrasound ($P>0.05$). In P2, no differences between RFI classes were observed for G:F and DMI as a percentage of BW ($P>0.05$), and small differences were observed for DMI (8.25 vs. 8.99 kg/d, $P<0.05$) and RFI (-0.28 vs. $+0.29$ kg/d, $P=0.06$). The ranking correlations for RFI and G:F measured consecutively in P1 and P2 were low to moderate ($r=0.11$–0.40). Low-RFI steers had lower requirements of metabolizable energy (ME) for maintenance (131 vs. 160 Mcal/kg $EBW^{0.75}$ d^{-1}, $P<0.05$), but no differences were observed for fat and protein gain, retained energy and efficiency of ME use for gain ($P>0.05$). No differences between low- and high-RFI steers were observed for carcass traits at slaughter; however, low-RFI steers had 8.1 kg less gastrointestinal fat than high-RFI steers. There were no RFI effects on meat shear force and the activities of μ-calpain, m-calpain and calpastatin ($P>0.05$). High-RFI steers had greater MFI in 1 d aged LM (53.9 vs. 40.8, $P<0.05$). The variation in feed efficiency between high- and low-RFI Nellore steers is related to differences in energy requirements and deposition of fat on internal organs. The ranking for feed efficiency is altered as cattle become older. The selection for improved RFI in Nellore cattle may reduce feed requirements for beef production without affecting meat tenderness and enzymatic activity of the calpain system.

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1. Introduction

Improving feed efficiency (FE) can increase the profitability (Cruz et al., 2010; Shreck et al., 2008) and diminish the environmental impact of beef production (Hegarty et al., 2007; Nkrumah et al., 2006). However, the selection for classical measures of FE, such as the feed conversion ratio (FCR), may lead to an increase in mature size that is undesirable in many circumstances (Archer et al., 1998a). For that reason, residual feed intake (RFI), a FE trait that is independent of growth rate and body size (Koch et al., 1963), has been broadly studied as a feed efficiency trait in beef cattle, and there is a growing interest among producers with respect to using RFI as a tool for genetic improvement (Wulfhorst et al., 2010).

The associations of RFI with biological processes affecting economically important traits have been reported in *Bos taurus* breeds (Herd et al., 2004; Richardson and Herd, 2004); however, there is a lack of research of this trait in *Bos indicus* breeds, particularly Nellore. *B. indicus* breeds are markedly present in tropical and subtropical areas where they may be more efficient than *B. taurus* (Elzo et al., 2009) because they are better adapted to such climates (Ferraz and Felício, 2010). This breed type differs markedly from *B. taurus* in terms of feed intake, growth rate, body composition, feed requirements, temperament and feeding behavior (Almeida, 2005; Lunstra and Cundiff, 2003; NRC, 1996; Prayaga, 2003; Schutt et al., 2009; Tuner, 1980), which supports the need for investigations specific to this breed because all of those characteristics can affect feed efficiency.

Other aspects of RFI associations with productive traits deserve further attention. For example, the linkage between variation in RFI and meat tenderness and the calpain system activity has not been conclusively determined (Baker et al., 2006; McDonagh et al., 2001). The calpain system plays an important role both in *postmortem* tenderization (Koohmaraie, 1994) and *in vivo* muscle growth (Goll et al., 1998), and it is associated with meat toughness as well as lean growth and feed efficiency in cattle (Morgan et al., 1993; Therkildsen, 2005). Any negative effect on meat quality as a consequence of the selection for improved RFI would be undesirable because of the importance of meat quality to consumers (Delgado et al., 2006; Shackelford et al., 2001). Furthermore, there is concern regarding whether the ranking of animals based on feed efficiency will change in response to ageing or consideration of the FE trait (Durunna et al., 2011). Thus, the assessment of feedlot performance over longer, consecutive feeding periods is needed to evaluate FE reranking of beef cattle.

Therefore, the aim of this work was to evaluate growth, carcass traits, feed efficiency reranking, body chemical composition, calpain system activity and meat quality in Nellore steers with high-RFI (less efficient) and low-RFI (most efficient).

2. Material and methods

2.1. Location of the study and the animals

All procedures involving animals were accomplished following the ethical principles required by the Brazilian Committee for Animal Experimentation (COBEA). The study was carried out at the College of Animal Science and Food Engineering of the University of Sao Paulo (FZEA/USP), Pirassununga, SP, Brazil. This region is characterized by a tropical climate with two well-defined seasons (wet summer and dry winter) and with an average annual temperature of 21.7 °C and rainfall of 1343 mm.

The cattle used in the experiment were the progeny of eight purebred Nellore sires that originated from the Nellore beef herd of the University of Sao Paulo. Castration occurred at weaning, when the cattle were approximately 8–10 months of age and 219 ± 22 kg BW. Between weaning and the beginning of the study, the cattle were kept in a single group, grazed in Brachiaria spp. pastures and provided with free-choice mineral mixtures. At the time of enrollment in the study, cattle were administered albendazol sulfoxide (Ricobendazole 10%, Ouro Fino, Cravinhos, SP, Brazil) and ivermectin (Ivomec 1%, Merial, Paulínia, SP, Brazil) to treat them for worms and botfly.

The study was divided into two consecutive feeding periods. In this paper, the first feeding period is referred to as P1, and the second feeding period is referred to as P2.

2.2. Feeding period 1 (P1)

Seventy-two steers that were 19 months ($\pm$29 d) of age with an average initial body weight (BW) of 334 ± 19 kg were studied. Thirty-six animals were housed in individual pens (5 m × 8 m), whereas the remainder was allotted to one of three group pens (10 m × 23 m) with Calan gates (American Calan Inc., Northwood, NH, USA). The pens were soil-surfaced and contained automatic water fountains and sheltered feed bunks.

During the adaptation period (21 d), steers received corn silage only (*ad libitum*), which was gradually exchanged for the experimental diet. Thereafter, the experimental diet (total mixed ration, 2.63 Mcal ME/kg and 14.3% CP in dry matter [DM] basis, Tables 1 and 2) was offered *ad libitum* at 800 h and 1700 h so that 10% refusals were allowed. The orts were weighed daily prior to the morning feed delivery to calculate the daily dry matter intake (DMI).

Hay and concentrate samples were collected weekly and composited on a monthly basis for chemical analyses.

Table 1
Ingredient composition of the experimental diet.

Ingredient	Dry matter (g/kg)
Coast cross, hay	254
Corn, ground	358
Soybean hulls	350
Soybean meal, 45% CP	22
Mineral premix[a]	6
Urea	10

[a] Minimum content per kilogram of mineral premix: 120 g Ca, 18 mg Co, 15 g P, 12 g Mg, 400 mg Fe, 22 g S, 297 mg Cu, 846 mg Mn, 2.5 mg Cr, 5 mg Se, 1100 mg Zn, 22 mg I, 110,000 UI Vit. A, 15,000 UI Vit. D, 100 UI Vit. D, 1000 mg sodium monensin.

Table 2
Chemical composition of the experimental diet.

Item	Dry matter(g/kg)
Dry matter (g/kg as fed)	732
Ether extract	23
Neutral detergent fiber	448
Acid detergent fiber	301
Ash	29
Crude protein	143
Rumen degradable protein[a]	98
Metabolizable energy (Mcal/kg)[b]	2.63

[a] Estimated according to NRC (1996).
[b] Estimated according to Weiss et al. (1992).

The hay DM content was determined weekly. The feed samples were dried at 55 °C for 72 h and ground to pass through a 1-mm screen. Dry matter, ash, crude protein (micro-Kjeldahl method) and ether-extract contents were determined according to AOAC (1990), and neutral and acid detergent fiber was determined according to Van Soest et al. (1991). The total digestible nutrients (TDN) was estimated according to Weiss et al. (1992), and the metabolizable energy (ME) content was estimated according to NRC (1996).

The daily dry matter intake (DMI) and average daily live weight gain (ADG) were recorded individually for a 70-d period to determine the RFI (Archer et al., 1997) and gain-to-feed ratio (G:F). The cattle were weighed in the morning on d 0, d 70 and each 21 d to determine the shrunk body weight (SBW) following 18-h feed withdrawal periods, during which the cattle were allowed free access to water. Concomitantly, the rump height (HGT) was measured, and the thoracic circumference was determined at d 70. The average daily gain was computed as the slope of the linear regression of BW on feeding days. The frame score was determined when cattle were 19 months old on average (Horimoto et al., 2006).

On d 0 and 70, the steers were scanned using a real-time Piemedical Scanner 200 VET (Pie Medical, Inc., Maastricht, The Netherlands) ultrasound instrument that was equipped with an 18-cm, 3.5 MHz linear array transducer. The ultrasound rib eye area (UREA) and subcutaneous backfat thickness (UBFT) were measured on the *Longissimus dorsi* muscle (LM) between the 12th and 13th ribs, and the ultrasound rump fat thickness (URFT) was measured on the *Biceps femoris* muscle. The images were collected and analyzed by an experienced technician using the Lince software (M&S Consultoria Agropecuária Ltda, Pirassununga, SP, Brazil).

The residual feed intake was calculated by regression of the DMI on the mid-test metabolic BW and ADG (Archer et al., 1997). The cattle were ranked on the basis of RFI, and the steers with the 12 highest and 12 lowest values were assigned to the high-RFI and low-RFI groups, respectively, with the remainder classified as the medium-RFI group.

2.3. Feeding period 2 (P2)

The high- and low-RFI groups were subjected to a subsequent feeding period (P2). These cattle were housed in individual pens (5 m × 8 m) and had free access to the same diet offered in P1 until they reached the targeted harvest weight (HBW) end-points, which had been randomly assigned at the beginning of P2. This resulted in nine different slaughter dates occurring between d 47 and 134 of P2. The treatments were balanced across slaughter dates.

2.4. Reranking of RFI and G:F between successive feeding periods

Spearman's rank correlation analyses were carried out among P1, P2 and the pooled period (P1+P2) for both RFI and G:F. For these analyses, RFI was recalculated separately in each feeding period for the high- and low-RFI groups. To calculate RFI and G:F over the entire feeding period (RFIpooled), DMI, ADG and mid-test $BW^{0.75}$ were computed again using pooled data from P1 and P2.

2.5. Body composition and energetics

At the beginning of P1, the empty-body chemical composition (EBC) of 10 steers was determined and assumed to be the initial EBC in calculations of the gain of the chemical components in the empty body weight (EBW). At the end of P2, the EBC was determined for the high- and low-RFI groups.

The EBC was estimated using the isotopic dilution methodology involving deuterium oxide (D_2O), which was adapted to the Nellore breed by Leme et al. (1994). The blood D_2O concentration was determined by laser absorption spectroscopy (Los Gatos Research Inc., Mountain View, CA, USA), and the deuterium space (D2OSp) was calculated. The percentages of water and fat in EBW were estimated using the calculated D2OSp from the equations by Leme et al. (1994), as follows:

$$\text{Water (\%)} = 65.9654+[0.0977 \times \text{D2OSp (kg)}]-[0.0909 \times \text{SBW (kg)}];$$

$$\text{Fat (\%)} = 93.92968-1.27598 \times \text{water (\%)}$$

The EBW percentages of protein and ash were estimated assuming the following protein:water and ash:water ratios in the fat-free EBW: 0.3009 and 0.0747, respectively (Leme et al., 1994). To calculate the EBW energy content and retained energy (RE), it was assumed that the heats of combustion of fat and protein were 9.385 and 5.539 Mcal/kg, respectively (Garrett and Hinman, 1969). The initial EBW was calculated by multiplying SBW by 0.8618. This coefficient was obtained by harvesting 10 steers with similar body weights (324 ± 16 kg SBW) and then weighing their gastrointestinal content. These steers originated from the same contemporary group; however, they did not participate in the study. The final EBW was estimated according to Aferri (2007), who had evaluated Nellore steers from the same herd and with similar SBW as those in the present study.

The requirement of ME for maintenance (MEm) was calculated according to Williams and Jenkins (2003). The partial efficiency of ME use for gain (k_g) was estimated by dividing RE by MEg.

2.6. Carcass and meat quality traits

The steers were slaughtered at the Experimental Abattoir of the University of Sao Paulo, and the carcass processing followed the common industry practices adopted in Brazil. The hot carcass weight (HCW) and kidney, pelvic and inguinal fat (KPI) weight were recorded. All removable fat from the gastrointestinal tract (GIT) was dissected and weighed. After a 24-h *postmortem* period, the carcass pH was measured, and the carcass was split into wholesale cuts. The LM section between the 12th and 13th ribs was exposed, and the marbling score, rib eye area (REA) and backfat thickness (BFT) were measured. The LM steaks were obtained from the exposed section for analysis of intramuscular fat content (ether extract, AOAC, 1990), Warner-Bratzler shear force, drip and cooking losses (AMSA, 1995) and the myofibrillar fragmentation index (Culler et al., 1978) of the aged (7 d) and non-aged (1 d) beef. The wholesale cuts were weighed and manually dissected into retail product yield (RPY, commercial cuts with 5 mm of covering fat), bones and trimmings (TRIM). The retail product and trimmings are expressed henceforth as a percentage of the cold carcass weight.

2.7. Determination of μ- and m-calpain and calpastatin activities

At slaughter, within 30 min after insensibilization, a 50-g muscle sample was obtained from the right side LM between the 12th and 13th ribs and was transported on ice to the laboratory. The μ-calpain and m-calpain were extracted, and their caseinolytic activities were determined according to Wheeler and Koohmaraie (1991), as modified by Sainz et al. (1992). The assays and blanks were performed in triplicate. Calpastatin was extracted according to Geesink and Koohmaraie (1999) and assayed against a known m-calpain activity, according to Sainz et al. (1992).

2.8. Statistical analyses

The data were analyzed for outliers (> 3 SD), homogeneity of variance (Hartley test) and normality of residuals (Shapiro-Wilk test). Outliers occurred in the body composition data (Table 6), because of errors during D_2O infusion procedure. These errors were a consequence of the intensive moving of temperamental animals in the chute.

The RFI effects on feedlot performance and carcass traits in P1 were analyzed using one-way analysis of variance in Proc GLM of SAS (version 9.1, SAS Institute Inc., Cary, NC, USA). There were no effects of housing type (group or individual pen) on any trait ($P > 0.05$, data not shown); therefore, housing type was not included in the statistical models that were used for data analysis. The mean values were compared using the Tukey–Kramer adjusted test. For responses in P2, the data were analyzed by a linear mixed model using restricted maximum likelihood and considering a completely randomized block design (slaughter date) in Proc Mixed of SAS. The slaughter date was considered a random effect. A linear mixed model for repeated measures in Proc Mixed was used to examine the fixed effects of RFI class, ageing period (1 and 7 d) and the respective interaction. The slaughter date (block) was also included as random in this case. Spearman's rank correlation analyses were carried out using the CORR procedure in SAS to evaluate the reranking of feed efficiency traits. A treatment difference of $P \leq 0.05$ was considered significant, and $0.05 < P \leq 0.10$ was considered to indicate a tendency.

3. Results

3.1. Feedlot performance and feed efficiency reranking

In P1, the mean, minimum and maximum values for RFI were 0.00, +1.54 and −2.72 kg DM/d, respectively, and the standard deviation for the trait was 0.69 kg DM/d.

There were no differences in P1 between RFI classes for frame score, final thoracic circumference, initial and final BW, metabolic mid-test body weight, age and ADG ($P > 0.05$). The high-RFI class presented higher DMI values in kilograms per day and in percentage of BW, higher RFI and lower G:F ($P < 0.001$) than the low-RFI class, whereas the medium-RFI class had intermediate values, between those of the other two classes (Table 3).

In P2, no differences ($P > 0.05$) between the RFI classes were observed for the final BW, days on feed, ADG, DMI in percentage of BW and G:F (Table 4). The high-RFI steers had higher DMI in kilograms per day ($P = 0.03$) than the low-RFI cattle, but only a tendency existed for differences between RFI classes regarding RFI in P2 ($P = 0.06$).

The ranking correlation between RFI and G:F in P1 and P2 (Table 5) showed that the RFI and G:F ranking changed, as observed by the moderate and low Spearman coefficients observed for the RFI1 × RFI2 and G:F1 × G:F2 relationships, respectively. The RFI1 was strongly correlated ($P < 0.001$) to the pooled RFI (P1 + P2) and moderately correlated to G:F1 ($P < 0.01$) but was not correlated with G:F2 ($P > 0.05$). The RFI2 was also correlated with RFIpooled ($P < 0.01$); however, it was correlated to a lesser degree when compared to RFI1. The correlation between G:F1 and G:F2 was quite low and non-significant ($P > 0.05$). The pooled G:F was moderately correlated to G:F1 ($P < 0.05$) and was strongly correlated to G:F2 ($P < 0.0001$).

3.2. Body composition and energy requirements

The dry matter and ME intakes throughout the entire study (P1 + P2) were lower ($P < 0.001$) for low-RFI steers than for high-RFI cattle (Table 6), but no RFI effects were observed on initial EBW, final EBW, body protein gain and body fat gain, retained energy and the efficiency of ME use for gain ($P > 0.05$). The high-RFI steers presented higher MEm than low-RFI cattle ($P < 0.01$).

3.3. Carcass traits

There were no differences ($P > 0.05$) between RFI classes in P1 (Table 7) for initial and final rump height,

Table 3
Feedlot performance of Nellore steers with high, medium and low RFI in the first feeding period (P1).

Traits	RFI class[b]			SEM[c]	$P>F$[d]
	High	Medium	Low		
n	12	48	12		
Age (d)	577	571	558	3.44	0.25
Thoracic circumference (cm)	185	183	181	1.15	0.66
Frame	8.46	7.67	8.01	0.18	0.29
Initial BW (kg)	340	334	336	2.16	0.50
Final BW (kg)	448	441	441	2.82	0.66
Metabolic mid-test BW (kg)	88.5	87.3	87.6	0.39	0.56
DMI (kg/d)	11.1a	10.1b	9.30c	0.11	<0.0001
DMI (%BW)[a]	2.80a	2.62b	2.39c	0.02	<0.0001
ADG (kg/d)	1.48	1.49	1.48	0.03	1.00
G:F (kg/kg)	0.134c	0.146b	0.159a	0.002	0.0009
RFI (kg DM/d)	0.85a	0.06b	−0.80c	0.07	<0.0001

[a] Ratio between average daily feed intake and mid-test body weight (BW).
[b] Within a row, means without a common superscript differ ($P<0.05$).
[c] Standard error of mean.
[d] Probability of a type I error.

Table 4
Feedlot performance of Nellore steers with high- and low-RFI in the second feeding period (P2).

Traits[a]	RFI class		SEM[a]	$P>F$[b]
	High	Low		
n	12	12		
Final BW (kg)	507	499	7.64	0.45
Days on feed	76	79	5.63	0.61
ADG (kg/d)	0.91	0.89	0.05	0.91
DMI (kg/d)	8.99	8.25	0.17	0.03
DMI (% BW)	1.86	1.76	0.04	0.15
G:F (kg/kg)	0.101	0.107	0.006	0.54
RFI (kg DM/d)	0.29	−0.28	0.20	0.06

[a] Standard error of mean.
[b] Probability of a type I error.

Table 5
Spearman's rank correlations between residual feed intake (RFI) and gain to feed ratio (G:F).[a]

Trait	RFI1	RFI2	RFIpooled	G:F1	G:F2	G:Fpooled
RFI1		0.40†	0.88***	−0.61**	−0.30	−0.51*
RFI2			0.70**	−0.65**	−0.24	−0.39†
RFIpooled				−0.77***	−0.39†	−0.60**
G:F1					0.11	0.49*
G:F2						0.87***

[a] RFI and G:F followed by 1, 2 and pooled were measured in the periods P1, P2 and P1+P2.
† $P<0.10$.
* $P<0.05$.
** $P<0.01$.
*** $P<0.0001$.

UREA, UBFT and URFT or for UREA and UBFT gain. The gain in URFT tended to differ among RFI classes ($P=0.06$).

At slaughter (Table 8), no differences ($P>0.05$) between treatments were observed for HCW, carcass dressing

Table 6
Energy intake, body composition and energy requirements in high- and low-RFI Nellore steers.

Item[a]	RFI class		SEM[a]	$P>F$[b]
	High	Low		
n	8	9		
DMI (kg/d)	10.1	8.73	0.22	<0.0001
MEI (Mcal/d)	26.6	23.0	0.53	0.0002
Initial EBW (kg)	291	291	2.92	0.93
Final EBW (kg)	481	473	8.97	0.45
Fat gain (g/d)	458	416	34.3	0.42
Protein gain (g/d)	190	187	6.10	0.79
RE (Mcal/d)	5.36	4.94	0.31	0.37
k_g	0.48	0.47	0.01	0.46
MEm (Mcal/kg $EBW^{0.75}$ d^{-1})	160	131	0.005	0.004

[a] Standard error of mean.
[b] Probability of a type I error.

percentage, REA, BFT, intramuscular fat, marbling score, retail product yield and trimming percentage. Additionally, the treatments did not affect the weights of the liver, heart, GIT and total viscera ($P>0.05$). Nevertheless, the low RFI cattle presented less fat on the GIT than the high RFI steers presented ($P=0.01$) and also tended to have lower KPI fat ($P=0.10$).

3.4. Meat quality and calpain system activity

No RFI class × ageing period interaction existed ($P>0.05$) for any meat quality traits. The meat samples at 7 d *postmortem* presented lower WBSF (4.63 vs. 5.56 kg) and greater MIF (71.6 vs. 47.4) than the non-aged samples (1 d postmortem) ($P<0.001$); however, the ageing period did not affect drip and cooking losses ($P>0.05$). The correlation between WBSF and MFI in this work was moderate to low ($r=-0.26$; $P=0.08$, $n=46$, data not shown). When the data were analyzed within ageing periods (Table 9), there were no RFI effects on

Table 7
Rump height and ultrasound carcass traits of Nellore steers with high, medium and low RFI in the first feeding period (P1).

Traits[a]	RFI class[b]			SEM[d]	$P>F$[e]
	High	Medium[c]	Low		
RHT (cm)					
d 0	141	140	140	0.36	0.35
d 70	145	144	144	0.38	0.58
UREA (cm^2)					
d 0	53.7	53.4	52.8	0.57	0.84
d 70	67.1	65.8	66.5	0.63	0.76
Gain (d 70–0)	13.0	13.0	13.1	0.36	1.00
UBFT (mm)					
d 0	0.68	0.53	0.41	0.09	0.68
d 70	4.37	4.02	3.70	0.15	0.43
Gain (d 70–0)	3.77	3.48	3.29	0.14	0.61
URFT (mm)					
d 0	1.46	1.78	1.67	0.16	0.76
d 70	7.51	7.54	6.14	0.27	0.16
Gain (d 70–0)	6.05	5.77	4.48	0.22	0.06

[a] d 0 and 70 stand for the first and the last experimental day in feeding period 1, respectively.
[b] Within a row, means without a common superscript differ ($P<0.05$).
[c] Animals with RFI between 0.5 standard deviation (SD) below and 0.5 SD above mean.
[d] Standard error of mean.
[e] Probability of a type I error.

Table 8
Carcass traits at slaughter and viscera of Nellore steers with high- and low-RFI.

Traits	RFI class		SEM[d]	$P>F$[e]
	High	Low		
Hot carcass weight (kg)	311	308	5.57	0.59
Carcass dressing	61.3	61.6	0.46	0.70
Kidney, pelvic and inguinal fat (kg)	6.25	5.63	0.19	0.10
Rib eye area (cm^2)	75.7	73.5	2.21	0.57
Backfat thickness (mm)	6.61	6.40	0.54	0.85
Marbling[a]	398	368	30.2	0.64
Intramuscular fat[b] (%)	2.71	2.41	0.23	0.54
Retail product yield (%)	62.0	62.7	0.57	0.58
Trimmings (%)	20.9	19.8	0.65	0.39
Liver (kg)	4.78	4.72	0.12	0.81
Heart (kg)	1.46	1.45	0.04	0.85
GIT (kg)	18.9	20.1	0.49	0.24
GIT fat (kg)	37.6	29.5	1.57	0.01
Total viscera[c] (kg)	31.6	33.1	0.65	0.27

[a] 300, Traces^0; 400, Slight^0.
[b] As is basis.
[c] Viscera included GIT (empty, free of removable fat), lungs, trachea, spleen, kidneys (free of removable fat), heart, pancreas, bladder, esophagus, and liver.
[d] Standard error of mean.
[e] Probability of a type I error.

WBSF 1 d and 7 d *postmortem* ($P>0.05$). The high-RFI steers had greater MFI in LM aged 1 d ($P<0.05$), but no differences in MFI were observed between RFI classes in the LM aged 7 d ($P>0.05$). No RFI effects were observed for pH; drip and cooking losses; activities of μ-calpain, m-calpain, and calpastatin; or the calpastatin:μ-calpain ratio ($P>0.05$).

Table 9
Carcass pH, Warner-Bratzler shear force, myofibrillar fragmentation index, drip and cooking losses and enzymatic activity of the calpain system in the Longissimus muscle of high- and low-RFI Nellore steers.

Trait	RFI class		SEM[a]	$P>F$[b]
	High	Low		
Carcass ph, 24 h postmortem	5.57	5.63	0.09	0.59
Warner-Bratzler Shear force (kg)				
1 d aging	5.65	5.35	0.26	0.56
7 d aging	4.79	4.50	0.25	0.55
Myofibrillar fragmentation index				
1 d aging	53.9	40.8	2.76	0.05
7 d aging	73.5	70.9	5.10	0.83
Drip losses (%)				
1 d aging	5.92	6.77	0.32	0.63
7 d aging	6.11	7.65	0.35	0.32
Total cooking losses (%)				
1 d aging	22.5	22.7	1.10	0.93
7 d aging	22.9	19.9	0.73	0.10
μ-Calpain (U/g muscle)	0.38	0.39	0.05	1.00
m-Calpain (U/g muscle)	0.50	0.48	0.03	0.85
Calpastatin (U/g muscle)	5.65	6.40	0.37	0.19
Calpastatin: μ-calpain	18.2	15.9	2.68	0.68

[a] Standard error of mean.
[b] Probability of a type I error.

4. Discussion

The low-RFI steers ate less and presented greater G:F without affecting the growth rate or increasing body size. The difference in feed consumption between efficient and non-efficient cattle was greater than 1 kg (dry basis)/d, whereas both groups had the same average weight gain. Furthermore, the independence of RFI with respect to body size could be observed through the similarity between RFI classes for frame score, thoracic circumference and rump height. The lower feed intake in more efficient cattle has been shown to positively impact profitability (Cruz et al., 2010; Shreck et al., 2008), and the independence of body size ensures that selecting for RFI will not affect herd mature weight or negatively increase feed requirements.

The concept of RFI with respect to its independence from both body weight and growth rate and its relationship with DMI and G:F can be observed throughout feeding period 1, but it cannot be observed during the successive feeding period. The differences in DMI and G:F between the low-RFI and high-RFI cattle during the first feeding period were 1.8 kg DM/d and 0.025 kg/kg, respectively; in the second feeding period, the difference in DMI decreased to 0.74 kg/d, and the G:F was statistically equal between RFI classes. These results show that the performance changed from the first to the second feeding period and are consistent with the reranking of animals observed from one feeding period to the next.

Contrary to the present study, other studies reported moderate to high correlations between the feed efficiency measured in different phases of life (Archer et al., 1998b, 2002; Arthur et al., 2001b; Nieuwhof et al., 1992).

These findings have been used to suggest that selecting more efficient cattle at younger ages could improve feed efficiency in the mature herd (Herd et al., 2003). However, the present results demonstrated that the relationships of RFI and G:F between the two consecutive periods were either moderate or small, indicating that the benefits of selecting superior animals for postweaning feed efficiency may be limited in other phases of the production system. Conversely, when comparing RFI and G:F, the ranking based on RFI was more consistent than that based on G:F, which suggests that RFI would be more appropriate for breeding purposes. In agreement with the present study, Durunna et al. (2011) reported small coefficients of correlation for RFI and G:F that were calculated in consecutive feeding periods.

Although feed efficiency did not remain consistent from one feeding period to the next, the cattle with the lowest RFI in P1 still exhibited lower energy intake than the high-RFI steers, and similar growth was observed in these two groups when the entire study was taken into account. The differences in RFI and feed intake were independent of the percentage of fat and protein in the body weight gain, resulting in no effects on retained energy. These results agree with other studies of high- and low-RFI steers from Angus crosses (Castro Bulle et al., 2007; Richardson et al., 2001) with respect to body chemical composition, and they indicate that low-RFI steers have lower energy requirements for maintenance. Lower energy requirements in low-RFI Nellore steers is consistent with decreased heat production in the most efficient Angus cattle (Basarab et al., 2003) and may be a consequence of several biological mechanisms, such as lower methane production during digestion (Nkrumah et al., 2006), lower physical activity (Barea et al., 2010; Luiting et al., 1994) and lower responsiveness to stress (Knott et al., 2008, 2010).

Throughout the first feeding period, a tendency for RFI effects on rump fat thickness gain may suggest differences in subcutaneous fat deposition across RFI groups. The tendency for a greater gain in rump fat thickness in the high-RFI steers is consistent with positive phenotypic and genetic correlations between RFI and rump fat that have been demonstrated in investigations with *B. taurus* breeds (Arthur et al., 2001a; Carstens et al., 2002; Lancaster et al., 2009) and Nellore bulls (Santana et al., 2012), and with greater backfat thickness in high-RFI Nellore steers in a previous study (Leme and Gomes, 2007). However, other studies reported low and non-significant correlations between RFI and carcass traits (Baker et al., 2006, Barwick et al., 2009; Carstens et al., 2002).

Greater fat deposition on the rump has been shown in Nellore steers when compared to the 12th–13th ribs region (Gomes et al., 2009), which is in agreement with the present findings. The differences in fat deposition between these two anatomical regions and the RFI effects on rump fat in the first feeding period of this study suggest that the inclusion of subcutaneous fat thickness in the RFI calculation to adjust for differences in body composition (Lancaster et al., 2009; Santana et al., 2012) should consider measurements made on the rump (*B. femoris* muscle) instead of measurements made on the *Longissimus* muscle between the 12th and 13th ribs. However, in the present study, neither backfat thickness nor rump fat thickness entered into the model for predicting dry matter intake (data not shown).

The results obtained at slaughter also indicate that RFI may be related to body fatness in Nellore cattle. Although no differences across RFI groups were observed for subcutaneous fat and trimmings, the low-RFI steers presented less fat on internal organs, as observed for the KPI and the GIT fat. The results of this study are also in agreement with those of other studies of Nellore cattle that reported greater subcutaneous fat thickness, KPI weight and trimmings percentage in high-RFI steers at slaughter (Leme and Gomes, 2007) and greater ultrasound rump fat thickness in high-RFI bulls (Santana et al., 2012). However, these results are different with respect to the body composition data collected in the current study because no differences between low- and high-RFI steers were observed for fat and protein percentages of body gain. In addition, other studies have reported no differences in visceral fat mass (Basarab et al., 2003; Cruz et al., 2010) or in backfat thickness between high- and low-RFI cattle (Almeida et al., 2004).

The variation in the GIT fat can partially explain differences in DMI between the most and least efficient animals. Assuming that the partial efficiency of ME use for fat retention was 0.75 (Williams and Jenkins, 2003), that the ME content of the diet was 2.63 Mcal/kg DM and that initial GIT fat mass was similar across individuals, the observed difference between high- and low-RFI cattle regarding GIT fat would be equivalent to approximately 230 g DMI/d if both feeding periods were taken into account (data not shown). This feed amount would be equivalent to more than 30% of the difference in DMI between RFI classes over the entire period, indicating that internal fat may be an important component of RFI variation in Nellore cattle. As the industry does not directly pay for non-carcass components, reducing the conversion of feed to visceral fat can be desirable.

The negative effects of the *B. indicus* breed on tenderness is primarily associated with the calpain system activity both *in vivo* and *postmortem* (O'Connor et al., 1997; Pringle et al., 1997; Wheeler et al., 1990; Whipple et al., 1990). In addition to its role in *postmortem* meat tenderization, the calpain system exerts important effects on skeletal muscle growth *in vivo* (Goll et al., 1998), affecting muscle protein turnover, energy requirements, lean tissue growth and gain-to-feed ratio in beef cattle (Castro Bulle et al., 2007; Oddy et al., 1998; Therkildsen, 2005). Therefore, the present study evaluated the relationships between feed efficiency and meat tenderness and the biological mechanisms underlying these relationships.

We observed that low-RFI cattle presented lower MFI in LM samples aged 1 d than high-RFI steers, which is in agreement with the findings of McDonagh et al. (2001). Lower MFI values would suggest that myofibrillar proteins in muscle of more efficient cattle are degraded to a lower extent as a consequence of lower protein turnover rates and that selecting for improved RFI may compromise meat tenderness. However, this is not supported by the results of calpain system activity and shear force determined in the present study and by results of sensorial panel and shear force reported for Angus steers (Baker et al., 2006). Therefore, studies with a trained sensory panel would be helpful in further investigations of whether RFI is related to meat tenderness in Nellore cattle.

5. Conclusion

Phenotypically low-RFI Nellore steers ate less, grew at similar rates and were more efficient when compared to high-RFI cohorts. Furthermore, there was no strong evidence that selecting cattle for low RFI will affect *postmortem* protease activities or compromise meat tenderness. Therefore, producers from tropical climates where *B. indicus* breeds predominate can benefit from raising more efficient cattle without affecting meat quality.

The differences in feed efficiency between the RFI classes in Nellore cattle were related to the deposition of internal fat and the energy requirements for maintenance, which were lower in the low RFI animals. The ranking based on RFI was altered throughout the post-weaning growth; however, the RFI was more consistent than the gain-to-feed ratio.

Conflict of interest statement

None.

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